WILEY **Diversity and Distributions**

Relationships between landscape constraints and a crayfish assemblage with consideration of competitor presence

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Abstract

Aim: Crayfish are globally diverse and one of the most important taxa in North American streams. Despite their importance, many species are of conservation concern and efforts to improve conditions are limited. Here, we address two major impediments to improving conditions: (a) our lack of knowledge of the interplay among natural landscape and human-induced changes; and (b) a very limited understanding of how species interactions affect overall crayfish distributions.

Location: Ozark Highlands ecoregion, USA.

Methods: We used both existing data and field-collected data to examine the relationships between 12 *Faxonius* species and physicochemical variables at multiple spatial scales. Data were analysed using a generalized linear mixed model. After fitting our environmental variables, we also considered possible relationships between species considered strong competitors and species occurrence.

Results: Our results indicated that elevation, lithology, an interaction between drainage area and anthropogenic disturbance, and the presence of strong competitors were associated with *Faxonius* occurrences. *Faxonius* occurrences were associated with assemblage-structuring variables: lithology and elevation. More interestingly, we found several patterns of interactions between drainage area and disturbance. The most common pattern among several species was a decline in occurrence in larger drainages when disturbance was high; however, longpincered crayfish (*Faxonius longidigitus*) was more likely to occupy large drainages as disturbance increased. Additionally, the presence of species considered strong competitors resulted in lower occurrence probability for many species, including two of the species classified as competitors.

Main conclusions: In addition to identifying the relationships between native species and assemblage-structuring variables, we show how the probability of species occurrences relate to interactions between disturbance and natural landscape features. Further, our results suggest competitor presence also plays a role in structuring distributions at the stream segment scale. Our findings emphasize the value of considering both competitor presence and interactions among landscape variables and disturbances in structuring crayfish assemblages.

KEYWORDS
anthropogenic disturbance, assemblage, competition, crayfish, *Faxonius*, multi-scale habitat

1 | INTRODUCTION

Understanding species distributions is challenging because they are based on a complex set of both abiotic and biotic interactions. Tolerances to certain environmental conditions (e.g., pH), dispersal ability and history (e.g., glaciation) and biotic interactions (e.g., competition, predation, parasitism) vary in space and time and interact in a myriad of ways, resulting in observed species patterns across the landscape. It is generally well accepted that climate and geology act as filters to dictate the aquatic species pool of a region (Poff, 1997; Tonn, 1990). For example, climate change could expand the range of some fishes (i.e., walleye [*Sander vitreus*], smallmouth bass [*Micropterus dolomieu*] and pugnose shiner [*Notropis anogenus*]) and contract the range of others (i.e., brook trout [*Salvelinus fontinalis*] and arctic char [*Salvelinus alpinus*]; Chu, Mandrak, & Minns, 2005). Additionally, these coarse-scale factors interact to determine the physicochemical conditions at finer scales (Frissell, Liss, Warren, & Hurley, 1986). For example, areas near one another, but with different lithologies, have distinct fish communities because of differences in water temperature, conductivity and pH (Neff & Jackson, 2012). In addition to natural landscape features, land use practices can interact with lithology and climate to alter the physicochemical conditions at finer scales, thereby affecting species distributions (Brewer & Rabeni, 2011; Stevenson, 1997). Both biotic and abiotic factors interact to contribute to observed species distributions, and the relative importance of each may depend on the spatial extent examined (MacArthur, 1972; as cited in Wiens, 2011). For example, the range limits imposed on a species may be partially due to thermal tolerances, but also due to the distribution of important prey items (Wiens, 2011). Evidence for biotic interactions in structuring distributions is most apparent at fine spatial scales. For example, gapped ringed crayfish (*Faxonius neglectus chaenodactylus* [Williams, 1952]) introductions change the crayfish assemblage (Rabalais & Magoulick, 2006) and damselfly assemblages are structured by the top predator (McPeek, 1990, 1998). However, biotic interactions can also occur over much larger landscapes (see overview of Wisz et al., 2013). A review of existing studies suggests that both biotic and abiotic components influence species distributions (Sexton, McIntyre, Angert, & Rice, 2009). There is an important link between the distribution of aquatic organisms and available conservation actions, but the data driving these actions are lacking for some ecologically important taxa.

Crayfish comprise a globally diverse group of invertebrates and are keystone species in North American streams. At least 382 crayfish species occur in North America, and an estimated 48% are at risk of extinction (Taylor et al., 2007). Threats to the persistence of many crayfishes include habitat alteration, narrow distributions and interactions with invasive crayfishes (Hamr, 2002; Taylor et al., 2007). Crayfish are both nutrient cyclers and food sources for many other animals (Momot, 1995; Nystrom, 2002). Crayfish are also consumed by more than 200 animals in North America including fishes, invertebrates, amphibians, birds and mammals (DiStefano, 2005). Changes in crayfish populations can significantly alter stream ecosystems by either reducing or increasing populations of algae, macrophytes, macroinvertebrates and fishes (James, Slater, Vaughan, Young, & Cable, 2015; Lodge, Taylor, Holdich, & Skurdal, 2000). Estimates of crayfish secondary production can exceed production of all other invertebrates combined (Rabeni, Gossett, & McClendon, 1994). We typically focus distributional studies of crayfishes at fine spatial scales (e.g., water temperature and salinity, Flinders & Magoulick, 2007; Noble & Fulton, 2016; Nystrom, 2002), but investigating multiple scales is important for effective conservation.

Crayfish distributions have been related to both abiotic and biotic conditions at coarser scales. Lithology and soils relate to crayfish distributions because of their influence on water chemistry, hydrology and crayfish burrowing success (Dyer, Brewer, Worthington, & Bergey, 2013; Nolen, Magoulick, DiStefano, Imhoff, & Wagner, 2014; Westhoff, Rabeni, & Sowa, 2011). Elevation and stream order are hypothesized drivers of crayfish distributions due to associated changes in stream discharge and water velocities (Dyer et al., 2013; Nolen et al., 2014). Crayfish also have varying tolerances to the physicochemical conditions associated with agricultural land use (Nolen et al., 2014; Westhoff et al., 2011). How biotic interactions among native crayfishes shape species distributions is rarely studied (James et al., 2015). Although, interactions between invasive and native species often result in the decline or extirpation of native species because of competitive disadvantages (Twardochleb, Olden, & Larson, 2013). Research examining assemblage structure rarely includes interactions between natural landscape factors (e.g., lithology) and human disturbance (hereafter referred to as disturbance) or the influence of hypothesized competitors. Understanding interactions between natural conditions and disturbance would aid in identifying areas of conservation concern (e.g., catchment location to develop mitigation strategies, O'Donnell, Baffaut, & Galat, 2008) and identifying interactions between species will provide a foundation for predicting the ecological consequences of crayfish introductions (James et al., 2015).

Our study objective was to examine relationships between the occurrence of 12 species of the *Faxonius* Ortmann, 1905 assemblage and multi-scale landscape factors, while considering the presence of competitors in the Ozark Highlands ecoregion, USA. The genus *Faxonius* is native to eastern North America (Hamr, 2002), comprises ~25% (88 species) of the crayfish fauna there (Crandall & De Grave, 2017) and represents approximately 21% of the imperilled crayfish species (Hamr, 2002). In addition to their ecological importance in lotic ecosystems, some species of *Faxonius* are also of economic and cultural interest (Hamr, 2002). For example, virile crayfish (*F. virilis* [Hagen, 1870]) is harvested commercially from the wild and several studies have evaluated its economic potential (Hamr, 2002). Recognizing the coarse-scale drivers of crayfish distributions allows managers to determine potentially invasive species (Westhoff et al., 2011), identify critical habitat (Westhoff et al., 2011) and focus their monitoring efforts (Wall & Berry, 2006).
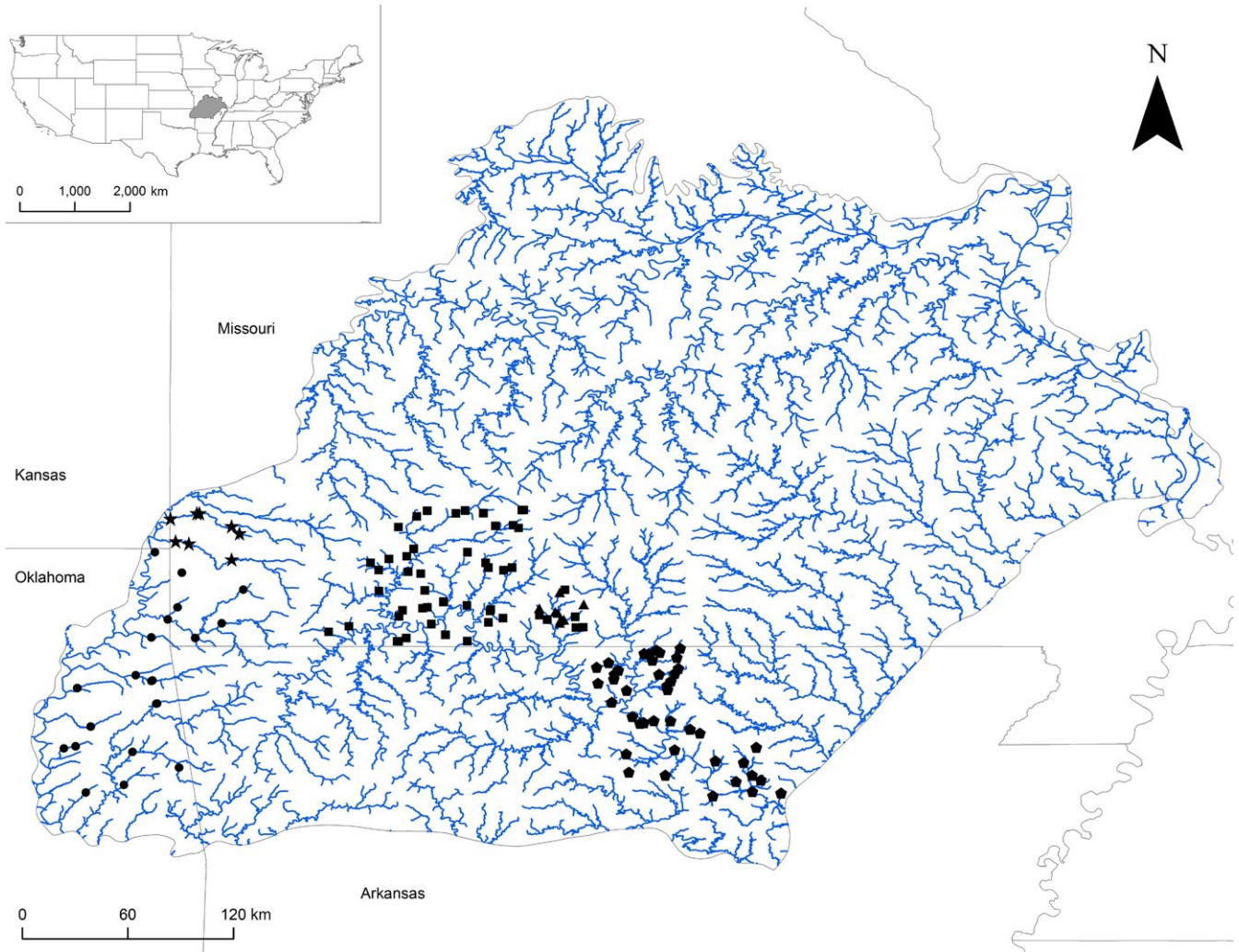
FIGURE 1 Locations of crayfish surveys in the Ozark Highlands ecoregion, USA. Different shapes identify data sources: stars = Allert, DiStefano, Schmitt, Fairchild, and Brumbaugh (2011); circles = field collections by the current study; triangles = Englebert, Taylor, and DiStefano (2015); squares = Westhoff, Guyot, and DiStefano (2006); pentagons = Wagner, Taylor, and Kottmyer (2010). See Supporting Information for Englebert et al. (2015) [Colour figure can be viewed at wileyonlinelibrary.com]

2 | METHODS

2.1 | Study area

The Ozark Highlands ecoregion encompasses portions of north-east Oklahoma, southern Missouri, south-east Kansas and northern Arkansas (Figure 1). The Ozark Highland ecoregion is characterized by limestone and dolomite lithologies and associated karst topography (Pflieger, 1996). Mean annual rainfall is 104–125 cm in the Ozark Highlands (Woods et al., 2005). Oak-hickory and oak-hickory-pine forest are the natural overstory vegetation of the Ozark Highlands, but many lowland areas have been converted to pasture (Woods et al., 2005). Ozark Highland streams support a diverse aquatic assemblage, which has evolved because of the variety of aquatic habitats (Pflieger, 1996). Twenty-five crayfishes are native to the Ozark Highlands, and 18 are members of *Faxonius* (Hobbs, 2001; Pflieger, 1996). Of these 18 *Faxonius*

species, 72% (13 species) are endemic to the Ozark Highlands ecoregion (Hobbs, 2001; Pflieger, 1996).

2.2 | Crayfish data

We obtained crayfish survey information from streams in the Ozark Highlands ecoregion from various sources (*n* = 134 sites, Table 1, Figure 1). We sampled crayfishes in the Neosho and Illinois river drainages from 2014 to 2015. Crayfish were sampled using tow-barge electrofishing during systematic and intensive fisheries surveys (a detailed approach is described in Mollenhauer, Mouser, & Brewer, 2017). Briefly, tow-barge electrofishing settings were pulsed direct current (DC), 60 Hz, and a 25% duty cycle. Voltage was adjusted to achieve a target power (W) that maintained a consistent electric field regardless of ambient water conductivity as described by Miranda (2009). Additionally, previous crayfish collection data from 2002 to 2013 were available for much of the White River and

Data source	Year(s) collected	Drainage(s)	Method	Stream length sampled
Westhoff et al. (2006)	2002–2003	Upper White River	Seine/kick seine	20 times bankfull width
Wagner et al. (2010)	2005–2006	White River	Hand netting	Stream segment
Allert et al. (2011)	2009	Spring River	Kick seine	3 riffle-run-pool sequences
Englebert et al. (2015)	2013	Little North Fork	Kick seine	20 times bankfull width
Field collections	2014–2015	Neosho and Illinois rivers	Electrofishing	3–5 riffle-run-pool sequences

TABLE 1 Crayfish surveys were conducted for this study and additional survey data were obtained from outside sources

Notes. We summarized the sample years, locations, sampling approach and stream length sampled relative to both our sample data (field collections) and existing data from other sources. See Supporting Information for Englebert et al. (2015).

Spring River basins. These existing survey data used either hand netting or seines to collect crayfish from a variety of habitats (Table 1).

All crayfish surveys were assigned to a stream segment (i.e., a length of stream between first-order tributary confluences) nested within USGS 12-digit catchment boundaries (https://nhd.usgs.gov/wbd.html). We imported global positioning system coordinates for each crayfish survey into ArcMap (10.2.1, ESRI, Red Lands, California). Data were pooled for stream segments with multiple surveys (*n* = 11). Stream segments nested in the same catchment shared coarse-scale characteristics.

2.3 | Environmental data

We determined drainage area, slope and mean elevation for each stream segment using National Hydrography Dataset flowlines (http://www.horizon-systems.com/NHDPlus/NHDPlusV2_home.php). Drainage area (km^2) was calculated two ways: (a) the total area drained upstream of the stream segment (hereafter drainage area); and (b) the area drained directly to the stream segment (hereafter segmentshed). We calculated segmentshed because it better represents local conditions, such as riparian corridors, that may directly relate to the biological integrity of streams (Sweeney & Newbold, 2014). We calculated slope as the difference in elevation between the upstream and downstream extent of the stream segment divided by the length of the stream segment. Mean elevation (m) was calculated as the mean of the upstream and downstream elevation of the stream segment.

We developed three variable sets that represented disturbance in the study area: (a) the proportions of different land use types for the stream segment including variables that represented agricultural land use (two categories: pasture and cultivated crops) and development; (b) a disturbance index that incorporated all

land use types for the stream segment scale; and (c) the same disturbance index at the catchment scale. Land use data were acquired from the 2011 National Land Cover Database (NLCD, https://www.mrlc.gov/). We used ArcMap to create a 500-m buffer centred around each stream segment (i.e., 250 m on each side) to determine proportional coverage of land use, where the number of pixels for each land use category was determined using the zonal histogram tool.

We developed variables for model inclusion that represented disturbances related to agriculture and other developed lands. We calculated both proportions of cultivated crops and pasture land use across stream segments to isolate disturbances to *Faxonius* assemblages that might be related to agriculture. We also created a variable that represented developed lands that did not encompass the aforementioned categories by combining proportions of (a) developed open space; and (b) low-intensity, medium-intensity and high-intensity development for each stream segment. We chose to combine the developed categories for two reasons: (a) broadly, we were interested in how any type of development influenced *Faxonius* distributions; and (b) medium- and high-intensity development made up extremely small proportions of each segment (i.e., <5%, except for three segments); therefore, we could not include separate categories in our analyses.

We were also interested in how overall human disturbance influenced the crayfish assemblage, so we calculated a disturbance index for each segment. The disturbance index was created by modifying the landscape development intensity index of Brown and Vivas (2005). Each land use category was first assigned a coefficient based on the level of disturbance (e.g., more disturbance resulted in higher coefficients). The categories detailed in Brown and Vivas (2005) were finer resolution compared to those available in the NLCD, thus allowing two or more categories to occur in one NLCD category.

TABLE 2 Main and interactive effects (±SE) and species-dependent coefficients (±SD) resulting from a generalized linear mixed model used to identify factors related to variation in *Faxonius* occurrence in the Ozark Highlands, USA

Species	Lithology other	Lithology dolostone	Lithology limestone	Elevation	Drainage area	Disturbance index	Drainage area × disturbance index	Presence of competitor
Main effect	−2.28 ± 1.49	−3.21 ± 1.50	−3.04 ± 1.28	−0.22 ± 0.63	0.40 ± 0.43	−0.08 ± 0.27	−0.29 ± 0.20	−0.94 ± 0.88
F. longidigitus	−3.67 ± 1.13	−1.32 ± 0.87	−4.50 ± 1.36	−0.23 ± 0.44	1.15 ± 0.35	0.89 ± 0.36	0.15 ± 0.17	−1.06 ± 0.73
F. luteus	−4.53 ± 1.22	−7.43 ± 2.15	−7.24 ± 1.72	1.25 ± 0.63	1.76 ± 0.60	0.68 ± 0.44	−0.54 ± 0.24	0.89 ± 0.92
F. macrus	−1.18 ± 0.81	−5.77 ± 1.98	−1.93 ± 1.18	0.39 ± 0.48	1.55 ± 0.45	−0.18 ± 0.28	−0.29 ± 0.18	−1.77 ± 0.83
F. meeki brevis	−1.05 ± 0.78	−5.75 ± 1.62	−1.81 ± 0.99	−0.16 ± 0.34	−0.29 ± 0.50	−1.15 ± 0.33	−0.76 ± 0.23	−1.18 ± 0.78
F. nana	−1.52 ± 0.84	−7.39 ± 2.46	−2.57 ± 1.32	0.44 ± 0.57	1.09 ± 0.56	−0.58 ± 0.34	−0.59 ± 0.24	−1.39 ± 0.97
F. n. chaenodactylus	0.80 ± 0.55	1.11 ± 0.56	−0.05 ± 0.58	0.06 ± 0.23	−0.04 ± 0.20	−0.40 ± 0.17	−0.18 ± 0.09	−0.79 ± 0.39
F. n. neglectus	0.62 ± 0.60	−0.66 ± 0.70	1.13 ± 0.63	−0.44 ± 0.26	1.10 ± 0.26	−0.16 ± 0.21	0.17 ± 0.12	−2.90 ± 0.45
F. ozarkae	−0.07 ± 0.59	−0.47 ± 0.64	−1.09 ± 0.68	0.02 ± 0.24	−0.17 ± 0.21	−0.34 ± 0.17	−0.37 ± 0.11	0.11 ± 0.48
F. punctimanus	−10.63 ± 2.06	0.82 ± 0.86	−7.29 ± 1.73	−5.20 ± 0.82	−2.12 ± 0.49	0.98 ± 0.41	0.55 ± 0.22	−3.50 ± 0.77
F. virilis	−0.11 ± 0.64	−1.64 ± 0.75	−2.33 ± 0.90	1.07 ± 0.36	0.52 ± 0.23	−0.16 ± 0.18	−0.47 ± 0.13	0.75 ± 0.63
F. williamsi	−1.58 ± 0.74	−2.77 ± 0.87	−3.20 ± 1.00	0.16 ± 0.33	−0.50 ± 0.36	−0.60 ± 0.23	−0.65 ± 0.18	0.24 ± 0.69

Notes. The intercept in the model was suppressed to improve interpretation of the lithology categories. Continuous variables were standardized to a mean of zero and variance of one; thus, coefficients represent estimated occurrence at mean levels. Coefficients are reported on a logit scale.

In these cases, we averaged the categories from Brown and Vivas (2005). For example, Brown and Vivas (2005) described several available pasture categories: woodland pasture (2.02), improved pasture without livestock (2.77), improved pasture low intensity with livestock (3.41) and improved pasture high intensity with livestock (3.74). All four of these categories were contained within one NLCD category ("pasture/hay"), and we averaged the four categories to obtain a single coefficient (2.99) for pasture. Our final coefficients were as follows: open-space development (1.83), low-intensity development (7.31), medium-intensity development (7.31), high-intensity development (8.67), pasture/hay (2.99), cultivated crops (4.54) and undisturbed (1.00). Undisturbed included all other land use categories (i.e., open water, barren land, deciduous forest, evergreen forest, mixed forest, shrub/scrub, herbaceous, woody wetlands and emergent herbaceous wetlands). Low- and medium-intensity development received the same coefficient because the NLCD separated those categories by proportion of coverage, but Brown and Vivas (2005) did not quantify coverage. Next, we multiplied the coefficient by the proportion of that category within each stream segment. The resulting values were summed across all land use categories to obtain a final disturbance index for each stream segment.

We examined lithology and disturbance at the catchment scale to understand their relationships with *Faxonius* occurrences. We chose to analyse lithology at only the catchment scale because we expected the effects of lithology on local conditions to occur at coarser spatial scales (e.g., pH; Frissell et al., 1986). Lithology was obtained from existing USGS spatial data (https://mrdata.usgs.gov/geology/state/). We used the identify tool in ArcMap to classify the dominant lithology within each catchment as dolostone (i.e., any lithology containing dolostone), limestone (i.e., any lithology containing limestone) or other (i.e., any other lithology). We also calculated a cumulative disturbance index for each catchment as described above for segments.

2.4 | Presence of strong competitors

Many crayfishes have the potential to become invasive if established outside their native ranges; however, successful invasions for some species have been documented. For example, ringed crayfish (*F. neglectus neglectus* [Faxon, 1885]), gapped ringed crayfish and virile crayfish are native to the Ozark Highlands, but have become established outside of their native range due to their environmental tolerance, high fecundity and large size (Filipová, Holdich, Lesobre, Grandjean, & Petrusek, 2010; Larson & Olden, 2010; Rabalais & Magoulick, 2006). Therefore, we hypothesized that the presence of these strong competitors (i.e., ringed crayfish, gapped ringed crayfish and virile crayfish) in a stream segment would influence the occurrence of other native crayfishes. Thus, we included an indicator variable that described the presence of a possible competitor (i.e., any of the three-aforementioned species) in each stream segment (see Section 2.5 below).

2.5 | Analyses

We included most crayfish species and subspecies encountered during the surveys in our analyses (Table 2). We excluded Meek's crayfish (*F. meeki meeki* [Faxon, 1898]) because it was found in only one stream segment. We included the subspecies ringed crayfish, gapped ringed crayfish and Meek's short pointed crayfish (*F. meeki brevis* [Williams, 1952]) because we were interested in potential differences in factors driving occurrence. For surveys that did not identify ringed crayfish to the subspecies level, we assigned crayfish to respective subspecies using distributions defined via genetic analyses (Dillman, 2008). Collections that identified subspecies also followed the distributions defined by genetic analyses. Although there is an intergrade zone for the two subspecies, the sample points where we assigned subspecies designations were well outside of the intergrade zone.

We examined relationships between *Faxonius* occurrence among stream segments and both multi-scale environmental variables and a biotic component using a generalized linear mixed model (GLMM). We fitted models using the package lme4 (Bates, Mächler, Bolker, & Walker, 2014) in the statistical software R (version 3.3.0; R Core Team, 2016). *Faxonius* occurrence was a binary response variable (i.e., we assigned a one if the species was encountered in the stream segment and a zero otherwise), and we specified a binomial error distribution with a logit link. The models included random catchment intercepts to broaden our scope of inference, account for pseudoreplication and accommodate the nested structure of our dataset (Wagner, Hayes, & Bremigan, 2006). Because all sampling gears have an associated bias, we also included random sampling method intercepts (electrofishing, seining or hand netting) in the models. We also treated species as a random effect in the models, where we included both random intercepts and random species by environment slopes (i.e., species × environment interaction terms). Treating species as a random effect allowed us to model all species simultaneously and provided more appropriate comparisons among species than treating species as a fixed effect or comparing single-species models (Jamil, Ozinga, Kleyer, & ter Braak, 2013). All continuous predictor variables were natural-log transformed due to right-skewed distributions and standardized to a mean of zero and a variance of one to improve interpretation of model coefficients and promote model convergence.

We assessed models using a forward selection similar to Jamil et al. (2013). Our initial (null) model comprised only the random intercepts catchment, sampling method and species. We then fitted models that each contained, as species-dependent random slopes, one of the ten environmental variables, interactions between each variable and lithology, and interactions between continuous variables with a Pearson's pairwise correlation coefficient ($|r| \leq 0.50$). The main effects of the predictor variables were not considered initially because the random model components partly accounted for them, and it allowed us to better isolate species-dependent relationships (Jamil et al., 2013). We retained the variables that most decreased SigAIC (Broman & Speed, 2002; Jamil et al., 2013).

SigAIC is a variant of Akaike information criterion (AIC; Burnham & Anderson, 2001) that uses a higher penalty factor (*c*) for increased model complexity, where we used $c = \chi^2_{1(0.10)} = 2.71$. We proceeded to add variables with this forward-selection process until the addition of variables no longer decreased SigAIC by at least one. After each step, we eliminated remaining continuous variables with $|r| \geq 0.50$ with retained variables, along with any interaction terms that included the eliminated variable. For the next modelling step, we determined if an indicator variable representing the presence of one or more strong competitor species explained additional variation in crayfish occurrence using the same SigAIC criteria. We assigned a zero to the indicator variable for all species if ringed crayfish, gapped ringed crayfish and virile crayfish were absent from the stream segment. Alternatively, we assigned a one to the indicator variable for all other crayfishes if any of the three-aforementioned species were present in the stream segment. The indicator variable for a hypothesized strong competitor received a zero for that stream segment if it was the only one of the three species found within that segment. Finally, we added the common slopes (i.e., main effects) for retained variables to complete the GLMM; however, these cannot be interpreted independent of the species–environment interactions.

For the final model, we assessed both fit and the amount of variation explained in *Faxonius* occurrence among observations. Because traditional residual plots are uninformative for models with binary response variables, we assessed model fit using binned residual plots (Gelman & Hill, 2007). We calculated marginal R^2 (variation explained by fixed effects only) and conditional R^2 (variation explained by both fixed and random effects; Nakagawa & Schielzeth, 2013; Johnson, 2014) for both the null model and the final model using the MuMIn package (Bartoń, 2016) in the statistical software R. The percentage variation in *Faxonius* occurrence explained by the final model was derived as [conditional R^2 (final model) − marginal R^2 (final model) − conditional R^2 (null model)] × 100.

We performed a 10-fold cross-validation (CV) to assess the performance of our final model. First, we divided our dataset into ten random subsets, which provided known states (i.e., observed species presence–absence at sites) to compare model predictions for each of the CV tests. The remaining 90% of the data served as the "training set" for each test, where we fitted models using the parameters included in our final model. We used linear combinations of model coefficients resulting from each training set to estimate occurrence probability for each observation in the test set based on associated predictor variable values. We did not consider the random catchment intercepts in the estimates to provide a more conservative evaluation of model performance (i.e., the species occurrence predictions were based only on modelled environmental relationships and gear bias). Each resulting probability from the linear combinations was approximated from the logit scale to a value between zero and one (Jørgensen & Pedersen, 1998), where we considered estimates ≥0.5 a predicted species occurrence. Lastly, we compared the predicted state to the observed state for each observation in the test sets.

3 | RESULTS

3.1 | Crayfish data

Eleven species and subspecies of crayfish were included in our final model (Table 2). The gapped ringed crayfish was the most common species and occurred in 78 stream segments. The next most common species (in descending order) were: the Ozark crayfish (*F. ozarkae* [Williams, 1952]) that was found in 59 stream segments, virile crayfish from 52 stream segments and ringed crayfish from 41 stream segments. Less common species were the golden crayfish (*F. luteus* [Creaser, 1933]), midget crayfish (*F. nana* [Williams, 1952]) and Meek's shortpointed crayfish that were found in three stream segments, in four stream segments and in six stream segments, respectively.

3.2 | Environmental data

Environmental variables at both the catchment and stream segment scales varied considerably (Table 3). Thirty-nine catchment variables were classified as dolostone, 48 were classified as limestone and six were classified as "other" lithology. Both the catchment and segment disturbance indices ranged from mostly natural (1.14 and 1.01) to highly disturbed (5.73 and 5.84). Most segments had little disturbance, but some were nearly all pasture or developed. Almost 80% of the segments (106 of 134) had small drainage areas (<200 km^2), but three segments had comparatively large drainage areas (>20,000 km^2). The segmentshed was typically small (<50 km^2). Slope among stream segments ranged from 0.00001 to 0.029. Elevation varied the least among segment-scale variables. At least one strong competitor species was encountered at 63 segments, where two competitors were encountered at 53 of these. All three competitor species were never encountered at the same stream segment.

3.3 | Analyses

Our final model included segment-scale elevation and competition, an interaction between catchment disturbance and segment drainage area, and catchment geology (Table 2). The most correlated variables in the final model were land use and elevation ($r = 0.37$, see Supporting Information Table S1 for correlations among all variables). The predictor variables explained 46% of the variation in *Faxonius* occurrence among observations. The conditional R^2 for the final model was 0.86, which suggests it accounted for a considerable amount of variation in *Faxonius* occurrence (i.e., either explained by predictor variables or controlled for by random intercepts). There was more remaining variation in *Faxonius* occurrence associated with sampling gear (variance ± *SD*: 0.86 ± 0.93) than unidentified catchment-level factors (variance ± *SD*: 0.24 ± 0.49). Seining, on average, tended to encounter more crayfishes (intercept 1.14 *SD* from the mean) than electrofishing (−0.03 *SD*) and hand netting (−0.73 *SD*).

Variation in *Faxonius* occurrence among stream segments was related to elevation and competition (Table 2). With other factors in the model held constant, longpincered crayfish (*F. longidigitus* [Faxon, 1898]), Neosho midget crayfish (*F. macrus* [Williams, 1952]), Meek's shortpointed crayfish, gapped ringed crayfish, midget crayfish and Williams' crayfish (*F. williamsi* [Fitzpatrick, 1966]) had no relationship with elevation (Table 2). Spothanded crayfish (*F. punctimanus* [Creaser, 1933]) was more likely to occur at lower elevations, whereas virile crayfish and golden crayfish were associated with higher elevations (Figure 2). For most species (i.e., longpincered crayfish, Neosho midget crayfish, Meek's shortpointed crayfish, gapped ringed crayfish, ringed crayfish, midget crayfish and spothanded crayfish), the presence of a strong competitor resulted in lower occurrence probability (Table 2). Golden crayfish, Ozark crayfish and Williams' crayfish showed no relationship with competitors.

TABLE 3 Average and the range of values for continuous environmental variables that were included in our study to characterize stream segments and catchments in the Ozark Highlands ecoregion, USA

Variable	Scale	Minimum	Maximum	Mean ± *SD*
Disturbance index	Catchment	1.14	5.73	1.92 ± 0.69
Disturbance index	Stream segment	1.01	5.84	1.86 ± 0.69
Cultivated crop	Stream segment	0	0.24	0.01 ± 0.03
Pasture	Stream segment	0	0.78	0.30 ± 0.22
Developed	Stream segment	6.74×10^{-4}	0.93	0.09 ± 0.13
Drainage area (km^2)	Stream segment	1.23	28637.21	705.41 ± 3724.60
Segmentshed (km^2)	Stream segment	6.30×10^{-3}	50.39	5.58 ± 8.80
Slope	Stream segment	1.00×10^{-5}	0.03	$6.20 \times 10^{-3} \pm 5.60 \times 10^{-3}$
Elevation (m)	Stream segment	73.66	443.38	249.13 ± 76.41

Notes. The disturbance index was calculated following Brown and Vivas (2005). (Land use data were obtained from existing geospatial data from the 2011 National Land Cover Database). Drainage area, slope and elevation were derived from the National Hydrography Dataset flowlines.

Only virile crayfish had a positive relationship with the presence of competitors (Table 2).

We observed four general patterns of crayfish occurrence in relation to the interaction between segment drainage and catchment disturbance. First, the occurrence probability of many species we examined (i.e., Ozark crayfish, Williams' crayfish, Meek's shortpointed crayfish and gapped ringed crayfish) increased with larger drainage area under low levels of disturbance, but declined in larger drainage areas under high levels of disturbance (Figure 3a). Additionally, both virile crayfish and midget crayfish had higher occurrence probabilities under low and moderate levels of disturbance when occupying larger drainages, but declined under high disturbance. Second, occurrence probabilities of the Neosho midget crayfish, ringed crayfish and golden crayfish were associated with higher occurrence probability in larger streams, regardless of disturbance (Figure 3b). Third, longpincered crayfish had a greater occurrence probability in larger, disturbed streams (Figure 3c). Lastly, the spothanded crayfish tended to occupy smaller drainages, but its occurrence probability remained relatively high in large, disturbed streams (Figure 3d).

Species showed varying relationships with catchment lithology (Table 2). Gapped ringed crayfish, longpincered crayfish and spothanded crayfish were more likely to occur in catchments characterized by dolostone, whereas ringed crayfish were more likely to occur in catchments characterized by limestone. All other species were more likely to occur in other lithology types.

We examined the final model and determined that model fit was adequate, and the predictive ability was good. The binned residuals confirmed good model fit. Approximately 95% of the binned residuals were contained in theoretical error bounds, and the plot did not reveal any concerning trends (Gelman & Hill, 2007). Based on the 10-fold CV, our model predicted correctly 86% of the time. The model tended to predict false absences ($n = 127$) more than false presences ($n = 77$; see Supporting Information Table S2). Additionally, the model made false predictions most often for Ozark crayfish, gapped ringed crayfish and virile crayfish (see Supporting Information Table S3).

4 | DISCUSSION

We show relationships between coarse-scale environmental variables and the *Faxonius* assemblage in portions of the Ozark Highlands ecoregion, while considering the presence of competitors. Crayfish distributions are often studied at a finer scale, focusing on factors such as life history and habitat use (e.g., DiStefano, Westhoff, Ames, & Rosenberger, 2016; Noble & Fulton, 2016). Studies that focus on the importance of finer-scale habitat features are useful, but would benefit from placement in the context of ultimate and intermediate controlling factors (Frissell et al., 1986; Poff, 1997). The relative importance of the patterns observed at fine scales may change when placed in the context of coarser scales, and vice versa. A few recent studies have examined crayfish distributions at a coarse scale (e.g., Dyer et al., 2013; Nolen et al., 2014; Westhoff et al., 2011), but have focused on one or a few species rather than an assemblage (but see
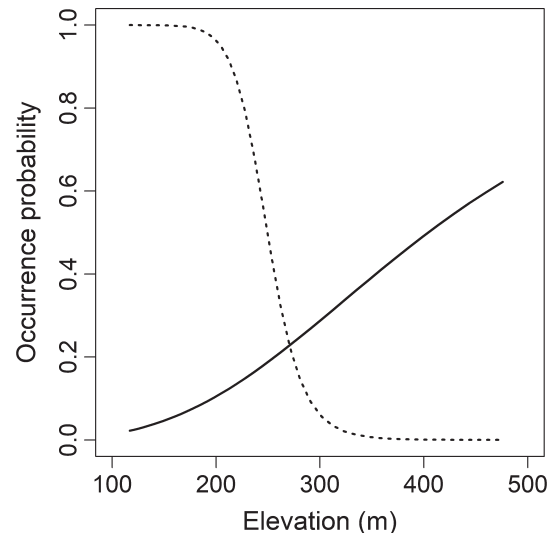

FIGURE 2 The relationship between *Faxonius* occurrence and elevation in the Ozark Highlands ecoregion, USA. Estimates were derived from a generalized linear mixed model used to identify landscape factors related to variation in *Faxonius* occurrence. Other variables included in the model were held at mean levels (except the categorical variable "geology" which was set to dolostone). Species are represented by a dashed line: spothanded crayfish *F. punctimanus*; and solid line: virile crayfish *F. virilis*

Magoulick, DiStefano, Imhoff, Nolen, & Wagner, 2017). Focusing on the *Faxonius* assemblage allowed us to show the trade-offs of landscape factors for different species, including those that were relatively rare.

We found that relationships between *Faxonius* occurrences and disturbance were dependent on conditions in the cumulative drainage area upstream of the stream segment. Disturbance effects are likely due to the cumulative conditions that occur in the upstream drainage that translate into local conditions that are not favourable to some crayfishes. Other studies have also demonstrated that increases in agricultural and urban land uses influence crayfish distributions (Frisch et al., 2016; Westhoff et al., 2011). For example, the stone crayfish *Austropotamobius torrentium* was negatively related to increased proportions of intensive grassland, which was attributed to fertilizer or manure polluting the stream (Chucholl & Schrimpf, 2016). Agricultural land use and urbanization often increase nutrient levels and alter both the sediment and flow regimes of streams (Heitke, Pierce, Gelwicks, Simmons, & Siegwarth, 2006; Poff et al., 1997; Short, Giddings, Zappia, & Coles, 2005; Wang, Seelbach, & Lyons, 2006). In many cases, we would expect human disturbance to be more pronounced in segments with larger drainage areas due to the accumulation of nutrients and sediment from upstream sources (Seitz, Westbrook, & Noble, 2011). Although interactive effects between landscape factors and stream size have been observed for fishes (e.g., smallmouth bass densities and interactions between soils and pasture land use, Brewer & Rabeni, 2011) and freshwater mussels (e.g., Wabash pigtoe [*Fusconaia flava*] tended to occupy upstream stream segments that were highly influenced by agriculture; see Supporting Information for Brewer &

FIGURE 3 The relationship between the occurrence of *Faxonius* and drainage area at varying levels of disturbance in the Ozark Highlands ecoregion, USA. Estimates were derived from a generalized linear mixed model, where other variables were held at mean levels. Lithology was "other," except for panel d, in which lithology was dolostone because spothanded crayfish *F. punctimanus* had extremely low occurrence probability in lithology other than dolostone. General patterns observed in these data via different species are shown in (panel a) Williams' crayfish *F. williamsi*; (panel b) ringed crayfish *F. neglectus neglectus*; (panel c) longpincered crayfish *F. longidigitus*; and (panel d) spothanded crayfish *F. punctimanus*. Disturbance is represented by: 1) solid lines (low disturbance, defined as 2 SD below the mean); 2) dotted lines (mean disturbance); and 3) dashed lines (high disturbance, defined as 2 SD above the mean)
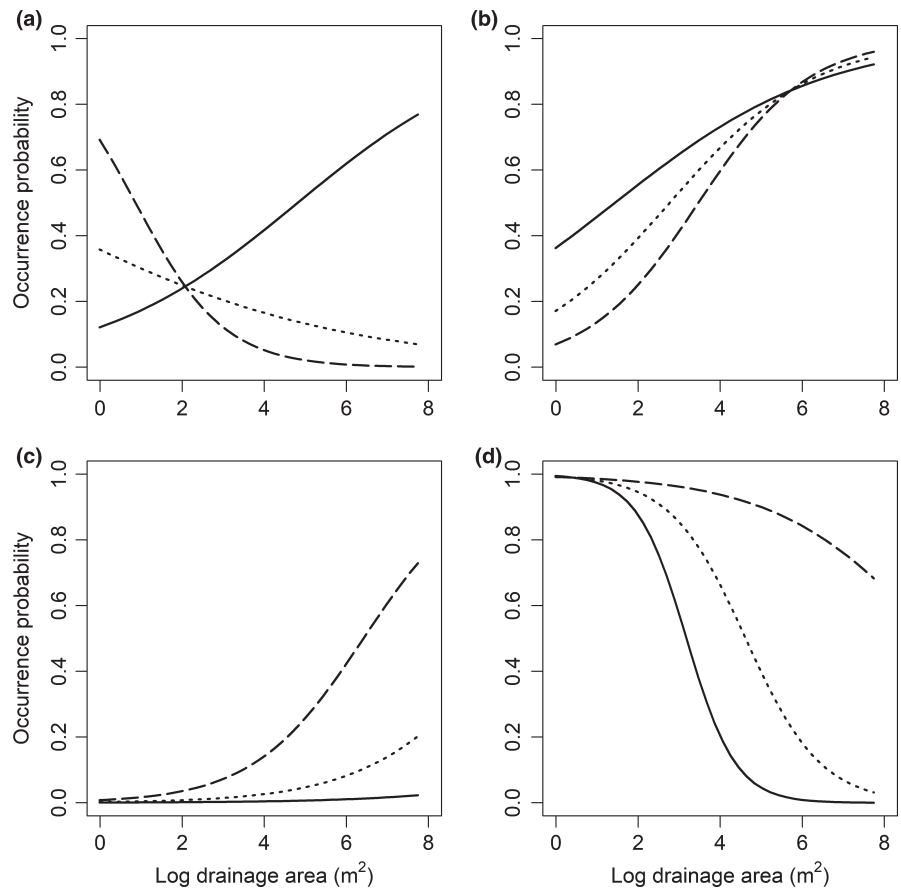
Powers, 2014), these types of analyses have rarely been performed for crayfishes.

We observed multiple patterns between *Faxonius* occurrence and catchment-scale disturbance. Several *Faxonius* species (e.g., Williams' crayfish) were negatively associated with larger drainage areas when the catchment was more disturbed, but positively associated under low disturbance. Williams' crayfish is a narrow-ranged endemic species typically found in areas with fast current, shallow depths, limited vegetation and cobble substrate (Wagner, Taylor, & Kottmyer, 2009; Westhoff, Guyot, & DiStefano, 2006). Thus, anthropogenic changes to the landscape may result in unfavourable conditions for species such as Williams' crayfish. We observed other species (e.g., ringed crayfish) that were positively associated with larger drainages, regardless of disturbance. The ringed crayfish is considered a habitat generalist and is a problematic invasive species (Schainost, 2011). Species like the ringed crayfish may be tolerant to the changes in local physicochemical conditions associated with the cumulative disturbance. Longpincered crayfish occurrence increased in streams with larger drainage areas and more disturbance. Longpincered crayfish are a long-lived species that display rapid growth (Pflieger, 1996).

Most crayfishes were negatively associated with the presence of a strong competitor species (i.e., ringed crayfish, gapped ringed crayfish and virile crayfish). All three crayfishes we considered competitors are dominant species that have either displaced other crayfishes in their native range (Pflieger, 1996) or altered crayfish assemblages

outside of their native range (Filipová et al., 2010; Larson & Olden, 2010; Rabalais & Magoulick, 2006); therefore, we hypothesized that they would affect the crayfish assemblage within their native range. The species we considered strong competitors are often the dominant species in streams where they are observed (Pflieger, 1996). Surprisingly, ringed crayfish and gapped ringed crayfish were negatively associated with the presence of other strong competitors. Virile crayfish tend to be larger, more fecund and have a wider distribution than both ringed crayfish and gapped ringed crayfish (Pflieger, 1996), which suggests they may be superior competitors (Larson & Olden, 2010; Peoples & Goforth, 2017). Of course, there are several population characteristics that contribute to the invasion potential of crayfish (e.g., aquaculture production, parthenogenesis; Souty-Grosset, 2016).

The distribution of *Faxonius* in the Ozark Highlands was strongly associated with catchment-scale lithology; interestingly, most species more likely to occur in lithology other than limestone or dolostone. Multiple lithology types (i.e., shale, sandstone and siltstone) were contained within the category "other," and we are unable speculate on what might be driving these patterns. Crayfish are typically distributed across a variety of lithologies and often associated with sandstone, shale and limestone areas that are typically basic with an abundance of inorganic ions in the water (Jay & Holdich, 1981). Ringed crayfish and gapped ringed crayfish were exceptions to this trend, with the former occupying segments in primarily limestone catchments and the latter occupying segments

in dolostone-dominated catchments. Lithology determines water chemistry and the dominant substrate of streams (Hynes, 1975). For example, limestone- and dolostone- dominated areas of the Ozarks are associated with cherty loam soils, which results in rocky stream beds and abundant dissolved solids (Brewer, Rabeni, Sowa, & Gust, 2007; Westhoff et al., 2011). Previous work has associated both ringed crayfish and gapped ringed crayfish with rocky streams that are free of silt (Pflieger, 1996).

We found that the occurrence of *Faxonius* members had different relationships with elevation. Virile crayfish were more likely to occur in higher elevation areas with other variables in the model held constant, whereas spothanded crayfish were more likely to occupy lower elevation stream segments. Elevation is a commonly used stream segment variable that represents coarse changes in channel characteristics. For example, nutrients, hydrology, sediment, (Allan & Castillo, 2007), substrate particle size (Dyer et al., 2013) and water temperature (Caissie, 2006) are all related to elevation. In our study, drainage area and elevation were not highly correlated, which suggests that the association with elevation may be related to either substrate or some other local physicochemical factor that we did not consider in our model (e.g., vegetation).

Imperfect sampling detection applies to most, if not all, species (Kéry & Schmidt, 2008), including crayfishes (Magoulick et al., 2017; Williams, Brewer, & Ellersieck, 2014); however, we were unable to directly account for species detection probabilities. Repeat surveys are required to model the detection process (MacKenzie et al., 2017), and these were available at only 11 stream segments. Alternatively, we accounted for general bias among gear types used in our study via random intercepts in the model. Given the observed strong relationships between *Faxonius* occurrence and environmental variables, we also feel that explicitly accounting for detection probability would not have changed our major findings (species associations with coarse-scale factors). Furthermore, it is preferable to use presence–absence in lieu of presence-only data. Although some observations are potentially false species absences, absence data should not be discarded because it can result in loss of important ecological information (Yackulic et al., 2013).

Our findings are useful for both management and conservation planning. Crayfish are popular as both fishing bait and pets, often resulting in non-intentional introductions (Chucholl, 2013; Lodge et al., 2000). From an invasive species management perspective, our findings provide important ecological information to help identify problematic crayfishes if introduced outside their native range and identify which systems might be most affected. For example, Capinha and Anastácio (2011) modelled the potential distribution of four invasive decapods and determined that an important national park was highly susceptible to possible invasion. Preventative conservation actions offer monetary savings when compared to both mitigation (Brooks et al., 2006) and eradication efforts (Allendorf & Lundquist, 2003). Our results also benefit agencies interested in conservation efforts because realization of natural constraints can save valuable resources. For example, focusing monitoring efforts in streams with the proper drainage area or elevation to harbour

a species would save valuable resources when attempting to identify critical habitat needs. Further, identifying the relationships with variables obtained from existing geospatial data can speed the assessment process over a large study area (i.e., environmental data that do not have to be collected in the field) and matches the resolution of crayfish data obtained from multiple studies within a stream segment. If the fine-scale mechanisms are also of interest, a follow-up study could be placed within the context of these coarser controlling landscape factors. Our results are also helpful in identifying basins with species more sensitive to changes in land use (i.e., anthropogenic disturbance). Thus, (a) monitoring efforts might target a few specific species; and (b) resources directed at buffers or other protective measures can target these locations. Future efforts would benefit by examining the interactions between other human stressors and natural basin characteristics and identifying the interplay among local physicochemical conditions (e.g., pool depths) within landscape constraints.

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BIOSKETCH

The authors' research is focused on identifying relations and mechanisms related to rare, declining or economically important aquatic species for which the causes and corresponding management responses are unclear. They conduct applied research on a wide range of lotic species to address specific conservation and management questions. Activities central to their efforts include determining population size, occupancy, demographics, distributions and providing a scientific basis to guide conservation and management actions. A complete list of publications can be found at https://www.coopunits.org/Oklahoma/People/Shannon_Brewer/Publication.

SUPPORTING INFORMATION

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